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# Vulnerability of Aquatic Communities to Invasive Fish Regulated by Prey Size and Nutrient Availability

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VULNERABILITY OF AQUATIC COMMUNITIES TO INVASIVE FISH REGULATED BY  
PREY SIZE AND NUTRIENT AVAILABILITY

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**Abstract:** The effects of invasive organisms on native ecosystems can be challenging to understand when their effects are moderated by environmental characteristics. Here, investigation evaluated the effects of western mosquitofish (*Gambusia affinis*) on native aquatic communities over a gradient of nutrient availability. Our study consisted of (1) a laboratory experiment that assessed how body size of three native amphibian larvae – Pacific chorus frogs (*Pseudacris regilla*), western toads (*Anaxyrus boreas*) and California newts (*Taricha torosa*) – influenced the risk of mosquitofish predation and (2) a two-month-long outdoor mesocosm experiment that evaluated the influence of mosquitofish simulating wetland communities across a gradient of nutrient availability. In the laboratory study, chorus frog larvae demonstrated a significant relationship between body size and survival. In the mesocosm experiment, mosquitofish significantly reduced overall amphibian survival compared to non-fish treatments, but the magnitude of these effects varied among amphibian species and nutrient condition. However, for both newts and toads, survival in the presence of fish occurred only (newts) or was higher (toads) in the high nutrient concentration, indicating an interaction between fish presence and nutrients. Correspondingly, amphibians in the high nutrient conditions grew more rapidly over the course of the experiment. Fish also sharply reduced zooplankton abundance and thereby enhanced primary production. Importantly, however, mosquitofish total survival of offspring also increased strongly (>300%) with elevated nutrient levels, presumably through bottom-up food web effects. These findings suggest that while increases in primary productivity can mitigate the direct effects of invasive fish on a sensitive native taxon (i.e., amphibians), nutrient increases may differentially benefit invasive fish and lead to a series of indirect effects throughout the community. Our study has practical implications for understanding how environmental variables influence interactions between native and nonnative species, which can

inform freshwater ecosystem management and conservation efforts focused on mitigating effects of invasive species.

**Key Words:** *trophic cascade, invasion ecology, paradox of enrichment, primary productivity*

## Introduction

Introduction of invasive species is one of the greatest threats facing native ecosystems (Esters et al. 2011; Kaefer et al. 2007; Wilcove et al. 1998). The often unregulated effects of invasive organisms can lead to declines in native biodiversity and significant economic losses. Despite the potential for deleterious effects, it is often difficult to accurately predict the magnitude of how an invasive species will affect native ecosystems because of environmental variability (Pettersen 2003). The effects of invasive species can be challenging to predict if these effects depend on characteristics of the environment, as invader success can vary sharply as a function of habitat (Simon and Townsend 2003). For example, in Italy, introduced red-eared sliders (*Trachemys scripta*) demonstrated higher reproductive success in warmer climates (Ficetola et al. 2009). Additionally, the American bullfrog (*Lithobates catesbeianus*) exhibited a longer breeding season and advanced gonad maturation in southern Brazil compared to its temperate home range (Kaefer et al. 2007). In the United States, foraging activity of the invasive fire ant (*Solenopsis invicta*) was strongly correlated with soil moisture and humidity (Kidd and Apperson 1984), with little to no foraging activity in soybean fields. At a smaller scale of invasion, an experimental approach identified that introduced non-native zooplankton varied in success, depending on both the presence of zooplanktivorous mosquito larvae and the availability of dead insects as food (Miller et al. 2002). All of these case studies indicate that the success of invasive species, and thus their potential effects on native communities, can vary with environmental characteristics.

Species invasions are especially prominent in freshwater habitats (Simon and Townsend 2003). Examples of freshwater invaders include the opossum shrimp (*Mysis relicta*) in Flathead Lake, United States, zebra mussels (*Dreissena polymorpha*) in the rivers and Great Lakes of the

United States, and introduced brown trout (*Salmo trutta*) in New Zealand have all demonstrated system-wide effects (Simon and Townsend 2003; Spencer et al. 1991). Freshwater systems represent discrete ecosystems (isolated by the terrestrial landscape) with wide environmental gradients. One of the most variable abiotic physical factors between freshwater ecosystems, and especially lentic waterbodies (still freshwater systems), is nutrient availability. The availability of nutrients in an ecosystem, including key limiting nutrients such as nitrogen and phosphorus, can strongly influence the composition of many ecological communities (Elser et al. 2011). Limited nutrients within a system often regulate organisms by controlling food availability (Hargrave 2006). For example, an increase in nutrients tends to promote primary productivity (development of organic mass through photosynthetic pathways) and therefore creates a “bottom-up” effect by subsequently promoting higher trophic levels (Caraco et al. 1990; Wootton and Power 1993). High primary productivity promoting increased herbivory would lead to a bottom-up effect. Incidentally, increased consumers of lower trophic levels would promote a top-down effect. Furthermore, lentic ecosystems are increasingly becoming disturbed by anthropogenic nutrient enrichment (e.g., agricultural fertilizers) (Downing et al. 1999; Eesters et al. 2003), which can lead to aquatic eutrophication and subsequent declines in biodiversity (Caraco et al. 1990; Correll et al. 1993).

To date, however, few studies have examined effects of invasive species across a gradient of nutrient availability (Burke and Grime 1996; Miller et al. 2002). Although a long-standing debate in ecology has focused on determining whether bottom-up effects of primary productivity or top-down effects of predators are more important in structuring food webs (Borer et al. 2005; Wootton and Power 1993), this framework has rarely been applied to understanding invasive species effects. Conceptually, a bottom-up effect through increased nutrients could propagate

through the food web leading to positive effects for invasive predators occupying higher trophic levels. For instance, in the Rhine River food invaders comprise approximately 90% of the macroinvertebrate abundance and are deemed ecological engineers (organism that modifies and/or creates new habitat) because of their strong role at facilitating both top-down and bottom-up direction on the native community structure (Leuven et al. 2006). Alternatively, increases in nutrients might alter native communities by increasing food availability or reducing competition, potentially mitigating negative effects of invaders. Given that increases in resources can also cause prey populations to grow exponentially, higher productivity could also function to destabilize predator populations. Rapid increase in prey abundance would sustain an unstable predator population (i.e., the paradox of enrichment – Abrams 1996; Rosenzweig 1971).

The present study was focused on the western mosquitofish (*Gambusia affinis*) that was introduced globally to freshwater ecosystems as a natural biological control agent for mosquitoes in the early 1900s and has become established as a widespread invader (Hulbert 1973). The introduction had anticipated benefits for human society through declines in the spread of insect-vectored diseases (insects that provide a medium for infection) through the consumption of mosquito larvae and other aquatic invertebrates (Farley 1980). However, adverse effects of mosquitofish have been documented in over 40 countries and every continent excluding Antarctica (Farley 1980; García-Berthou 1999). Originally native to the watershed of the Gulf of Mexico (Krumholz 1948), mosquitofish have a generalist diet and consume virtually everything smaller than itself, an advantageous trait in new environments (Farley 1980). Equally important, the fish exhibits high fecundity, a short life cycle, and broad tolerance to water properties such as temperature, salinity, pH and dissolved oxygen (Farley 1980; García-Berthou 1999). Despite the prevalent literature on mosquitofish direct competition via predation on native species (Caraco et

al. 1990), little is known about what environmental factors influence mosquitofish success in introduced ecosystems.

The experiment studied how nutrient availability altered the effects of mosquitofish on a native aquatic community consisting of amphibians, aquatic invertebrates, zooplankton and algae. The study consisted of (1) a series of laboratory feeding trials to measure the relationship between amphibian body size and predation susceptibility and (2) an outdoor mesocosm experiment to evaluate the effects of invasive fish on wetland community structure along a productivity gradient. We expected that variation in primary production would alter the strength of mosquitofish effects on native communities. Our guiding hypotheses included: (1) increased primary productivity would increase amphibian growth rates, thereby reducing the susceptibility of amphibians to predation by fish, (2) increased primary productivity would increase habitat complexity through plant and algal growth, which would allow native species more refuge from nonnative fish predators, (3) increased nutrients would promote higher abundances of herbivores and primary consumers (e.g., zooplankton, snails, aquatic insects), which would provide more alternative prey for nonnative fish, thereby reducing predation pressure on native amphibians.

## **Materials and Methods**

*Laboratory experiment.* – This experiment was conducted at the Hopland Research & Extension Center in Mendocino County, California, USA from May to July 2012. Each replicate included 10 amphibian larvae and 3 non-gravid female mosquitofish. Amphibians were collected as larvae from local ponds absent of mosquitofish and held in a plastic container containing 1 L of aged tap water. Three size classes were used of the Pacific chorus frogs (*Pseudacris regilla*), three size classes of western toads (*Anaxyrus boreas*), and two size classes of California newts



(*Taricha torosa*) (with five replicates per size class). Developmental stage (Gosner 1960) and snout-to-vent length (SVL) were recorded from a subset of representative animals (Table 1). Survival of amphibians was measured each hour over an 8 h period. At the end of each trial, the mosquitofish were euthanized in a bath of MS-222 and SVL of mosquitofish were recorded.

*Mesocosm experiment.* – The experiment entailed a  $2 \times 2$  factorial experiment manipulating nutrient availability (low and high) and mosquitofish presence (present and absent) in an outdoor mesocosm array. Each treatment was replicated 5 times for a total of 20 mesocosms. The four treatments included low and high nutrient concentrations crossed with mosquitofish presence or absence. The treatments assigned to each mesocosm were determined from a random number generator. The mesocosms were Rubbermaid livestock watering tanks filled with 378 L of well water and equipped with drain holes below the rim to allow drainage from rainfall. Each mesocosm was placed two meters apart and covered with a screen lid to prevent unintended emigration and immigration. The nutrient concentrations mirrored natural aquatic systems in California and were informed by previous fieldwork (Johnson et al. unpublished) and previous research of how freshwater systems release P (Caraco et al. 1990). The nutrient concentrations reflected stoichiometric ratios of N and P in natural ponds and were adjusted for the volume of individual mesocosms (378 L). Inorganic P ( $\text{H}_2\text{PO}_4$ ) and N ( $\text{NaNO}_3$ ) were both added such that the concentrations in the high nutrient treatments were four times higher than the low nutrient treatments. The inorganic P and N nutrient supplements were based upon the mesocosm volume (378 L): the low nutrient treatments were 0.0316g and 0.750 g and the high nutrient treatments were 0.126 and 3.00 g. The results indicated a low and high output of 0.0185 and 0.327 and (TDN) 0.272 and 0.991 (TDP). Inorganic nutrients were added

(dissolved in 40 L of water) to each treatment every eight days. Algae were added 24 h after initial nutrients were added. Algae was collected from the Upper Dorm Pond and Parson's Creek at the Hopland Research Station by collecting surface-level algae with a D-frame dipnet (0.5-m opening  $\times$  0.5-cm mesh). Large zooplankton (primarily cladocerans and copepods) were collected from the Upper Dorm Pond and Hog Pond using a dip net (569  $\mu$ m mesh net).

After 14 days, the following invertebrate taxa were added to each mesocosm to better simulate a natural wetland community: snails (5 *Helisoma* sp. and 5 *Physa* sp.), backswimmers (10 *Notonecta* sp.), water beetles (5 *Dytiscidae* sp.), damselflies (10 *Coenagrionidae*), mayflies (15 *Baetis* sp.), dragonfly larvae (5 *Tramea* sp.), giant water bugs (3 *Belostoma* sp.), and benthic amphipods (20 *Gammarus* sp.). Two days later, amphibian larvae were collected from local ponds (absent of mosquitofish): 15 Pacific chorus frogs (Gosner stage = 26; SVL =  $4.04 \pm 0.09$ ), 20 western toads (Gosner stage = 27.4; SVL =  $8.74 \pm 0.20$ ) and 10 California newts (SVL =  $13.82 \pm 0.48$ ). Finally, mosquitofish were added in a 4 male (SVL =  $33.05 \pm 0.87$ ) to 3 female (SVL =  $39.05 \pm 0.81$ ) ratio.

Two sterile tiles (15 x 15 cm) were placed in each mesocosm to collect periphyton (mixture of algae, bacteria and other detritus attached to a surface) growth. In each mesocosm, the tiles were raised above the substrate on PVC pipe (5 cm in height) to prevent dead organic matter from covering the periphyton growth. Every 10 days, 3.3 cm<sup>2</sup> periphyton was removed from each ceramic tiles. The extracted periphyton sample was allowed to oven dry for 24 h to record the dry mass. The final periphyton sample growth (6 x 40 cm) samples were collected from the height of the mesocosm walls; these data served to compare periphyton with the initial periphyton tile growth recording at the onset of the. Every ten days, phytoplankton abundance was measured indirectly as chlorophyll fluorescence with a laboratory fluorometer (Turner

Designs, Sunnyvale, California, USA). At the end of the study, zooplankton abundance was measured based on samples collected with a tube sampler (70 cm in length  $\times$  5 cm in diameter, five combined samples per mesocosm). The samples were preserved in ethanol for later identification and quantification.

*Laboratory experiment analysis.* – We fit each hypothetical survival outcome for each amphibian larvae over 8 h period as a specific generalized linear mixed-effects models (GLMM) with corresponding survival responses (yes or no) in a binomial distribution using the lme4 package in *R* (Zuur et al. 2009). Individual containers were assigned as the random effect of individual replicates (uncontrolled variability between larvae within each container). Body size was assigned (Gosner stage and SVL) as fixed effects. These parameters allowed determination of significant relationships between body size and the likelihood of mosquitofish predation.

*Mesocosm experiment analysis.* – For all mesocosm response variables, analyses were conducted on mesocosm means. Two-way MANOVAs with mosquitofish and nutrient concentration as independent variables were used to analyze mesocosm data on response variables of native amphibian species (Gosner stage, SVL, and wet mass). One-way ANOVAs were used for zooplankton (abundance), snail (abundance), notonectid (abundance), periphyton (mass), phytoplankton (concentration), and amphibian survival (percentage of initial). A two-way MANOVA measured the fish responses (wet mass and total survived offspring) with nutrients. Two-way MANOVAs were used to determine if any interaction was present between nutrients and fish for phytoplankton fluorescence and periphyton growth.

## Results

*Laboratory results.* – Chorus frog larvae demonstrated a significant relationship between survival and the presence of mosquitofish, as well as showing that survival increased along with larval body size (Fig. 1A; GLMM,  $Z = -4.24$ ,  $P < 0.00001$ ). Western toad larvae survival did not exhibit a significant relationship with body size (Fig. 1C) (GLMM,  $Z = -0.242$ ,  $P = 0.888$ ) nor did survival of the California newt larvae (Fig. 1B; GLMM,  $Z = 0.588$ ,  $P = 0.557$ ). Western toad larvae displayed the highest survival, 80% for size one and 92% for size two (Fig. 1C). We observed 0% survival for chorus frog larvae in size class one, 58% survival for size class two, and 100% for size classes three and four (Fig. 1A). California newt survival was 84% for size class one and 76% for size class two (Fig. 1B).

*Mesocosm results.* – The presence of fish interacted significantly with nutrient concentration to determine toad survival, such that the negative effects of fish were dampened under high nutrient conditions (Fig. 2A; ANOVA,  $F_{3, 19} = 20.12$ ,  $P < 0.0001$ ). Concurrently, the presence of fish significantly interacted with nutrient concentration to determine toad time to metamorphosis, SVL and wet mass (Fig. 2B; MANOVA,  $F_{9, 48} = 1.313$ , Pillai's Trace  $P < 0.0005$ ). In contrast, newt survival only exhibited a significant interaction between fish and high nutrient concentration, indicating that fish presence suppressed nutrient effects at lower nutrient concentrations (Fig. 2C; ANOVA,  $F_{3, 19} = 10.65$ ,  $P < 0.01$ ). Following the same trend, the presence of fish at high nutrient concentrations yielded significant newt morphological responses (Fig. 2D; MANOVA,  $F_{2, 7} = 49.44$ ,  $P < 0.0001$ ). Remarkably, in the presence of fish no chorus frogs survived (Fig. 2E; ANOVA,  $F_{3, 19} = 88.00$ ,  $P < 0.0001$ ). However, in treatments without fish, chorus frog morphological responses demonstrated significant relationship with nutrient

concentration, suggesting that increased nutrient concentrations facilitated increased growth rates (Fig. 2F; MANOVA,  $F_{3,6} = 5.05$ ,  $P < 0.0443$ ).

With respect to other members of the aquatic community, increases in nutrient levels strongly enhanced effects on cladoceran (benthic zooplankton grazer) density whereas mosquitofish presence reduced other zooplankton (Fig. 3A; ANOVA,  $F_{1,19} = 5.42$ ,  $P < 0.0317$ ). For instance, in treatments with fish, zooplankton abundance was reduced by over ten-fold. However, neither nutrients nor fish had any significant effects on snails or other invertebrates including: *Helisoma* sp. (abundance and total wet mass; MANOVA,  $F_{1,9} = 0.7981$ ,  $P = 0.3977$ ), *Physa* sp. (MANOVA,  $F_{1,9} = 0.7593$ ;  $P = 0.408$ ), amphipod (abundance; ANOVA,  $F_{3,19} = 0.676$ ,  $P = 0.590$ ), and notonectid (abundance; ANOVA,  $F_{3,19} = 0.9630$ ,  $P = 0.4342$ ).

*Primary productivity responses.* – At the bottom trophic level, increases in nutrients significantly promoted increased primary productivity in both periphyton and phytoplankton. For example, periphyton tile mass (June 17, 2012) (Fig. 4A; ANOVA,  $F_{3,11} = 4.9111$ ,  $P = 0.0320$ ) and periphyton wall mass (July 13, 2012) (Fig. 4B; ANOVA,  $F_{3,19} = 2.4475$ ,  $P = 0.0167$ ) both indicated a significant growth increase in the presence of fish. This suggests the top-down effects of fish predation on herbivores (e.g., amphibian larvae) release primary producers. Subsequently, phytoplankton fluorescence (July 7, 2012) (Fig. 4C) also demonstrated significant density increases with the presence of fish (Fig. 4C; ANOVA,  $F_{3,19} = 3.524$ ,  $P = 0.0392$ ). Additionally, in the presence of fish, phytoplankton fluorescence was 26% greater in the high nutrient treatments.

*Mosquitofish responses.* – The experiment yielded increased mosquitofish success both in fecundity and overall wet mass as a function of nutrient concentrations (Fig. 5A; MANOVA,  $F_{3, 19} = 255.85$ ,  $P < 0.0001$ ). The strong fish success suggests that increased nutrients facilitated a bottom-up effect for additional primary consumers and thus additional prey items (e.g., zooplankton, macroinvertebrates). The total number of surviving mosquitofish offspring increased by >300% (Fig 5B; ANOVA,  $F_{3, 19} = 34.57$ ,  $P < 0.001$ ), and total wet mass increased 28% from low nutrient treatments. In high nutrient treatments, mosquitofish had an average of 18 offspring, and in low nutrient treatments, demonstrated an average of 4. There was a 69% increase in total fish wet mass from low to high nutrient treatments.

## Discussion

Human introductions of non-native species have had variable consequences on earth's ecosystems. Although introduced species can have adverse effects on native ecosystems, the complex process of species introductions limits the predictability of their impacts on new communities (Pettersen 2003). Part of this complexity is due to variation in environmental conditions. Variable conditions of both environment and invader determine consequences for native systems (Miller et al. 2002). Therefore, understanding the interaction of both invader and environmental variability can lead to greater understanding of invasive species impacts on native systems.

Western mosquitofish have been widely reported to cause adverse effects on native species within freshwater ecosystems (Hulbert et al. 1972). Because of mosquitofish's rapid reproduction and voracious feeding strategy, which can include attacking animals several times their own body size, mosquitofish have been shown to negatively affect amphibians (Gamradt

and Kats 1996; Preston et al. 2012). Other native invertebrates, including copepods, beetle larvae, crustaceans, and even surface dwelling ants and spiders, have been shown to be affected by mosquitofish introductions (Bence 1988; Hulbert and Mulla 1973; Hulbert et al. 1972; García-Berthou 1999; Hayes and Rutledge 1991). In California, mosquitofish have exhibited adverse impacts on native California fauna. For example, studies have evaluated mosquitofish predation on both the endangered red-legged frog, (*Rana aurora draytonii*) (Lawler et al. 1998) and the endemic fairy shrimp (Leyse et al. 2003). However, few studies have investigated how the effects of mosquitofish may vary with changing environmental conditions.

By integrating both a laboratory experiment and an outdoor mesocosm study, we were able to evaluate changes in wetland community structure in the context of both invasive mosquitofish and changes in nutrient concentrations. In the laboratory study, we recorded effects of amphibian species and the size of the amphibian larvae in relationship to predation by mosquitofish. Larger size classes exhibited higher survival for only chorus frog amphibian larvae. While mosquitofish consumed individuals of all three species, chorus frogs appeared to be most vulnerable to attack and also exhibited the strongest relationship between prey body size and predation.

This trend seen in chorus frog larvae may indicate increased survivorship is associated with size refugia, as recorded in a similar laboratory study that with insect predators (Anderson et al. 2001). This relationship also follows the gape-limited feeding of the mosquitofish (Bence and Murdoch 1966). The California newt and western toad demonstrated no significant relationship between body size and mosquitofish consumption by which most likely indicates, that other ecological variables influenced toad and newt larval survival. It is important to note,

however, that the size classes used among species could not be completely consistently, suggesting caution in over-interpreting between-species differences.

One important factor likely influencing larval survival in relationship to body size is toxicity variation. Relative to the chorus frog, the California newt and western toad are significantly more unpalatable, a successful anti-predator quality (Preston et al. 2012; Gunzburger and Travis 2005). It is important to note, however, that sublethal attacks to the limb and tail of amphibian larvae were not recorded here. Such attacks, which have been observed by mosquitofish in other studies (Goodsell and Kats 1999; Lawler et al. 1998; Gamradt and Kats 1996), could be important, especially over longer time scales when even toxic species suffer reduced performance as a result of with injury.

In the mesocosm experiment, we examined the individual and interactive effects of mosquitofish and nutrient concentrations on simulated aquatic communities, which included primary producers, zooplankton, macroinvertebrates and amphibians. Consistent with the lab study, chorus frog larvae exhibited the greatest survival declines in the presence of fish.

Interestingly, however, there was a significant interaction between nutrient concentration and fish presence in terms of their effects on newts and toads. The significant increase in wet mass and later developmental stage indicates that higher nutrient concentration facilitated an increased growth rate. The cause of increased amphibian survival with increased nutrient concentration could have several contributing factors. First, the bottom-up effect of added nutrients most likely supported increased amphibian herbivory, promoting increased growth rates and greater capacity for amphibians to achieve size refugia. Diverse algal communities have been noted to support higher chorus frog larvae diet and therefore increased growth rates (Kupferberg 1997). Consistent with the explanation, the study demonstrated that amphibians in



high nutrient condition achieved higher body size. With greater body sizes larvae may have reached size refugia (body size threshold that prevents predation) as demonstrated in laboratory conditions. Alternatively, the increase in nutrients may have increased the availability of alternative prey, such as zooplankton and invertebrates. Alternative prey can function to mitigate the effects of mosquitofish on sensitive taxa such as amphibians (Farley 1980; García-Berthou 1999; Goodsell and Kats 1999). Correspondingly, zooplankton abundance increased by over ten-fold in the high nutrient condition (without fish present), but showed no such increase when fish were present, suggesting a sharp effect associated with predation.

Importantly, however, changes in nutrient concentrations also had remarkably strong effects on the mosquitofish themselves. The experiment also detected increased fish reproduction and total wet mass with increased nutrients. This indicates that mesocosms exhibited mutual bottom-up effects and top-down effects during the experiment. It is likely that the increased alternative prey selection not only increased amphibian survivorship, but also sustained more mosquitofish offspring. Although we predicted the bottom-up-effects from increased nutrients would support alternative prey items, we did not anticipate the increase in primary production and secondary consumers to support such a marked elevation in fish reproduction. The significant increase in total survived fish offspring (>300%) and total wet mass (27%) support the notion that increased nutrients supported fish fecundity. Mosquitofish can become cannibalistic in resource-limited systems, although there may have also been lower production of offspring because adults were food-limited (Meffe and Crump 1987). The experiment demonstrated that increased nutrients had an overall strong effect on increased primary producers (phytoplankton and periphyton), leading to increased primary consumers (zooplankton and invertebrates) as well increased herbivore size (amphibians), which overall prompted increased

fish abundance. Although this experiment was relatively short-term, invasive fish fecundity could lead to an overall unstable community composition from excessive top-down pressures on the system. The strong fish success response alludes to the paradox of enrichment phenomenon: a sudden increase in primary consumers supports an even stronger growth in predators, which in long-term can lead to an unstable food web from exhausting top-down predation (Abrams and Walters 1996). This work is important for projecting the maximum carrying capacity for introduced predators on a system. In addition, the present study serves to support the overlapping effects of nutrient additives and non-native predators on a native community.

From an applied perspective, this study has implications for evaluating invasive fish effects on native wetland systems along a gradient of primary productivity not only for freshwater ecology but also wildlife management. The results indicate that highly productive ponds will also promote high mosquitofish fecundity, at least in the short term. It is crucial for invasive species management to understand effects on more than one or a few native species. Moreover, understanding the environmental characteristics that facilitate mosquitofish colonization still remains unclear. This research improves the understanding of how abiotic factors influence freshwater ecosystem composition. Future research should analyze the effects of invasive species and other abiotic factors on wetland community structure (e.g., dissolved-oxygen, pH and salinity). Further research into the variability of invader success with change in abiotic factors will improve the knowledge of how communities affect success of invasion.

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Table 1. Morphology measurements (Gosner stage and SVL) recorded for three native amphibian larvae and non-gravid female mosquitofish in laboratory feeding experiment.

Species	Gosner Stage (Mean)	Snout-to-vent length (mm) (Mean $\pm$ SE)
<i>Anaxyrus boreas</i>		
Size Class 1	26	4.82 $\pm$ 0.23
Size Class 2	28.9	15.46 $\pm$ 0.69
Size Class 3	37.7	13.85 $\pm$ 0.28
<i>Taricha torosa</i>		
Size Class 1	n.a.	11.84 $\pm$ 0.24
Size Class 2	n.a.	15.47 $\pm$ 0.67
<i>Gambusia affinis</i>	n.a.	33.88 $\pm$ 0.61

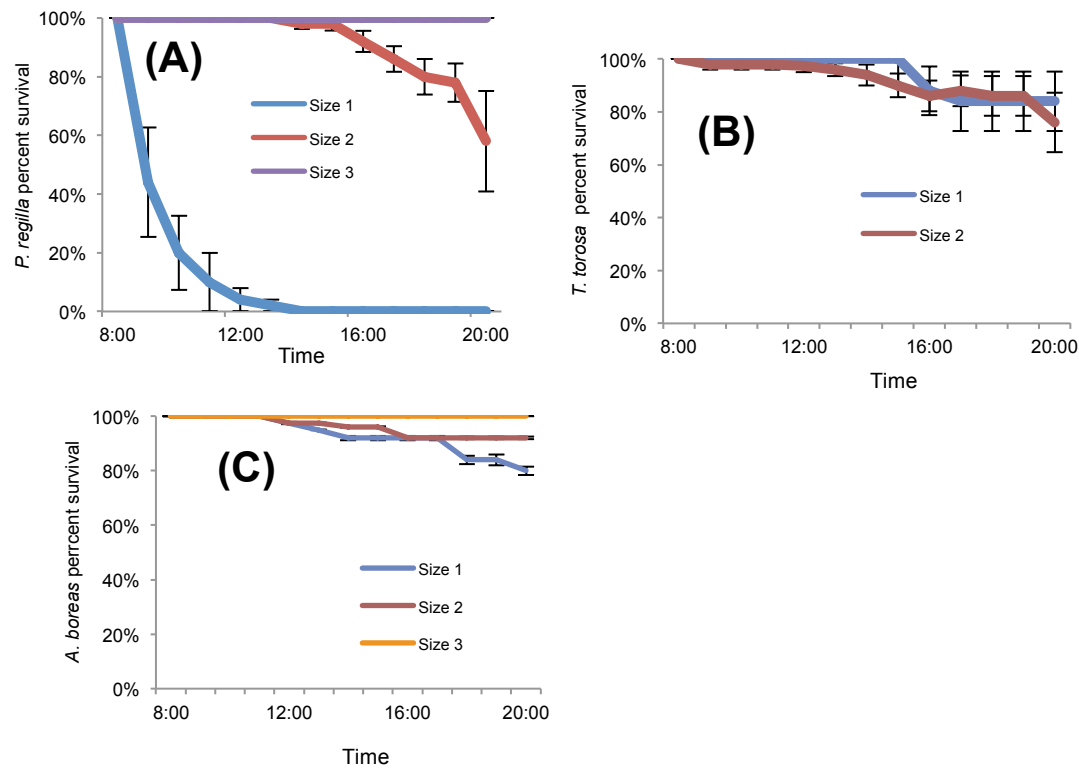


Fig. 1. Body size classes of three native amphibian larvae, (A) Pacific chorus frog (*Pseudacris regilla*), (B) California newt (*Taricha torosa*), and (C) western toad (*Anaxyrus boreas*) as influenced by mosquitofish predation over the course of a day in a laboratory setting. All lines represent means for size classes with standard error.

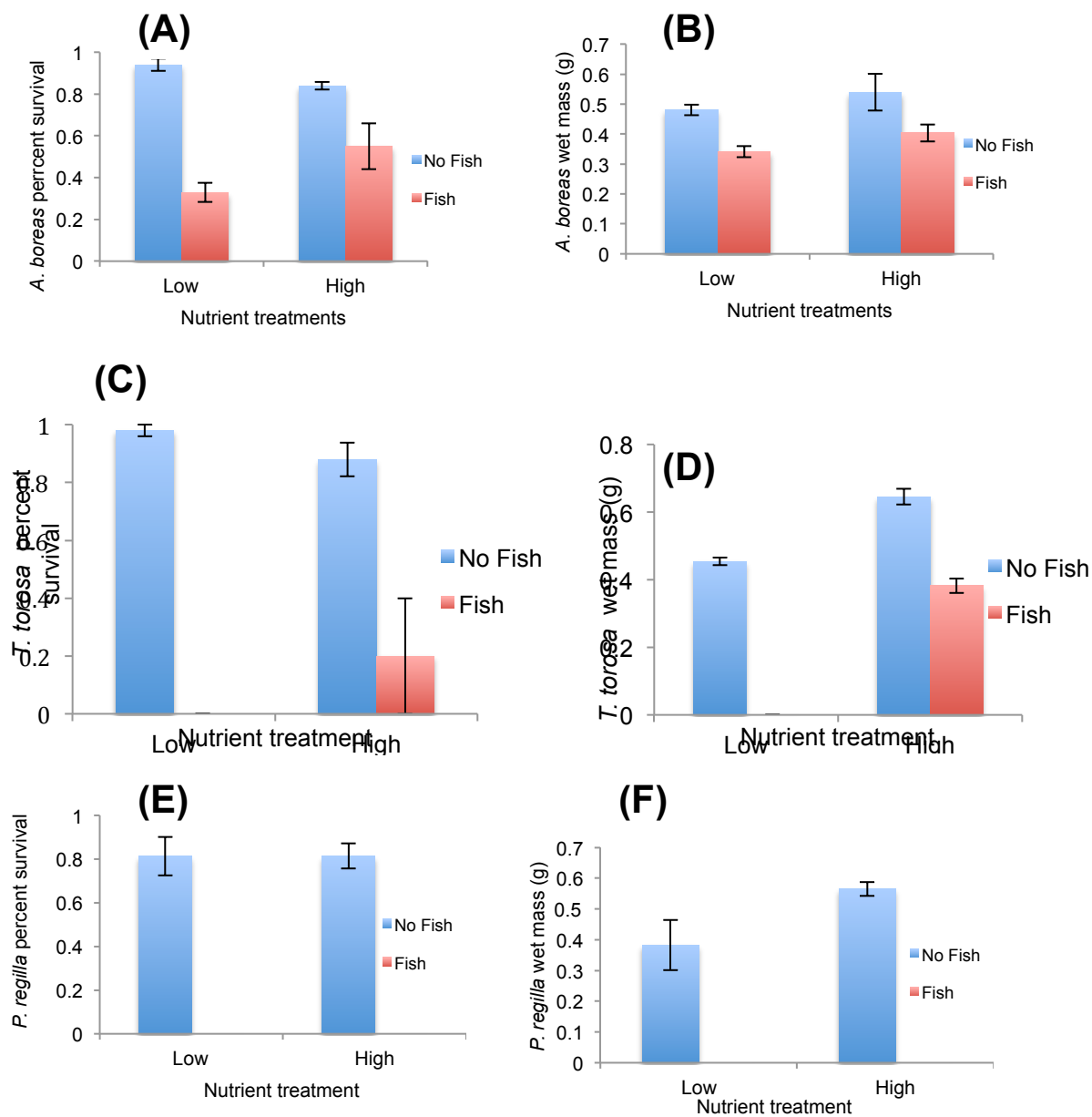


Fig. 2. Percent survival and wet mass for three amphibian larvae under fish and nutrient treatments in a field experimental mesocosm. Means with standard error.

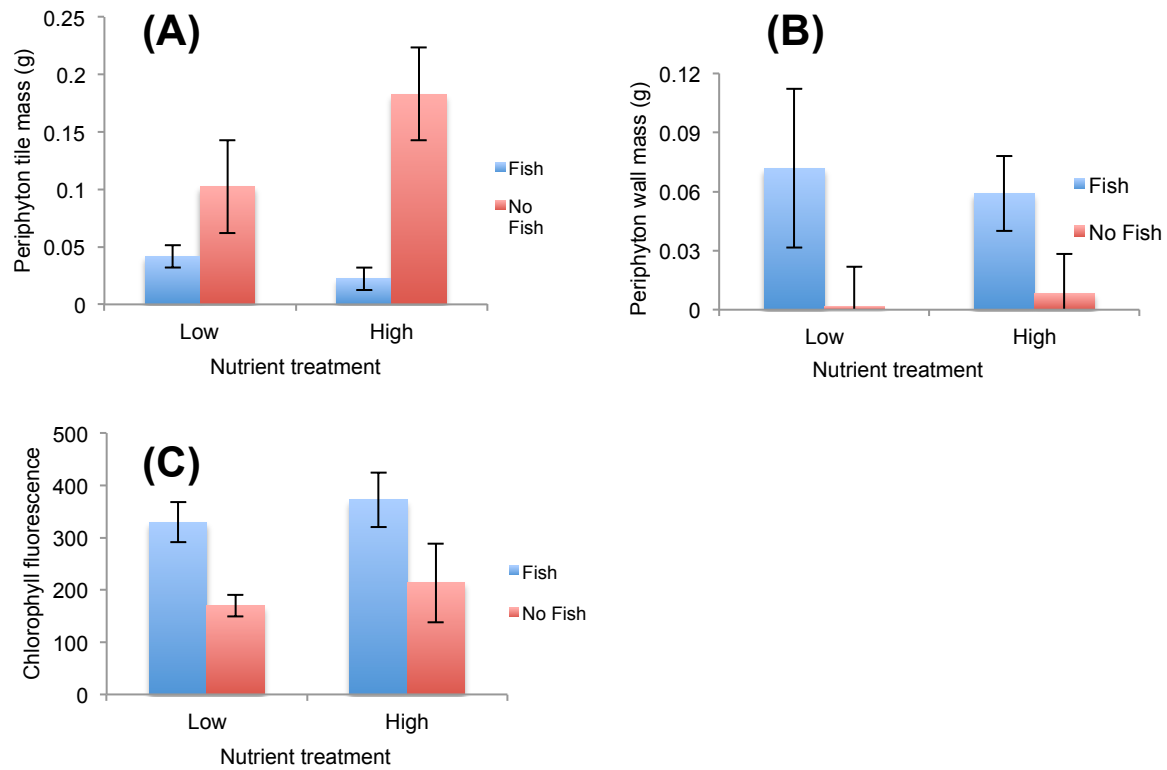


Fig. 3. Individual samples of periphyton dry mass with nutrient treatments and phytoplankton fluorescence for both nutrient and fish treatments in a field experimental mesocosm. Means with standard error.

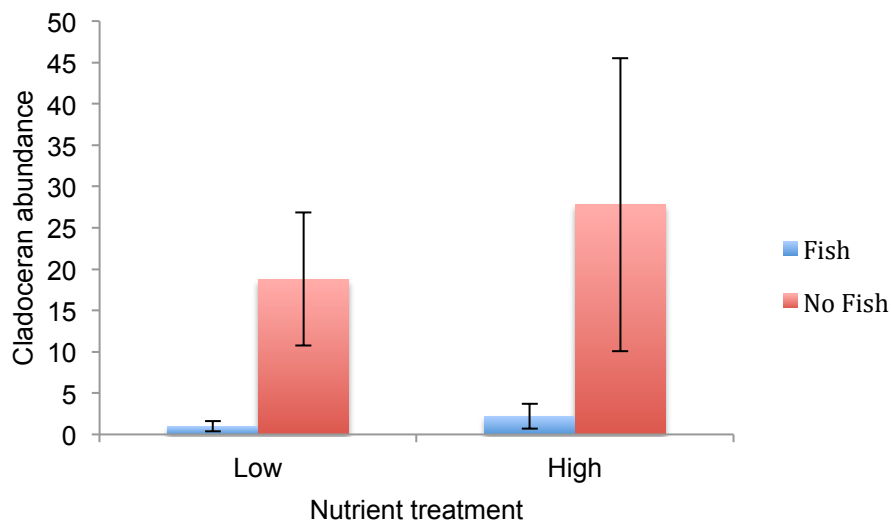


Fig. 4. Field experimental mesocosm results cladoceran for both nutrient and fish treatments abundance. All bars represent means with standard error.

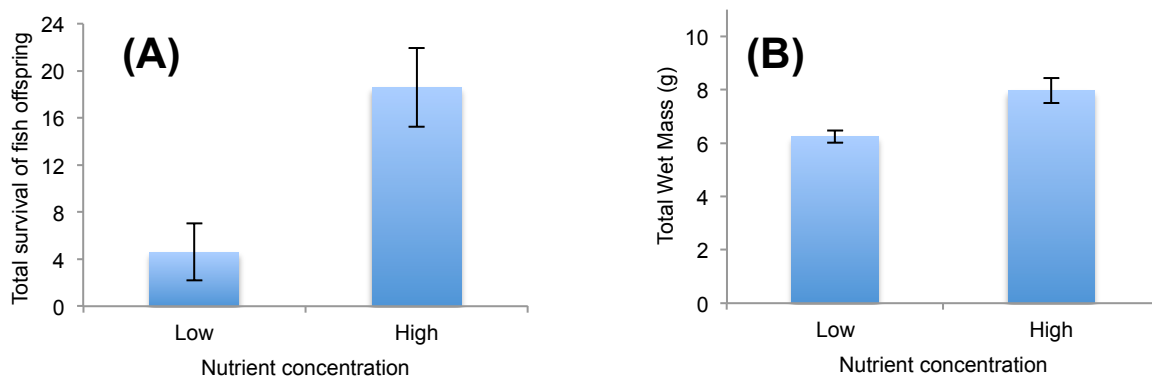


Fig. 5. Total offspring survival of fish offspring and total wet mass for field experimental mesocosms. Metric means with standard error.